

Manatee Metabolism and Its Influence on Distribution in Florida

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ABSTRACT

The metabolic rate of three captive manatees was measured at different water and air temperatures. The animals responded metabolically to cold water (15–20°C), but not to cold air (10–20°C). Average metabolic rates in the thermal neutral zone ($T_1 \cong 24^\circ$) were 15–22% of predicted weight-specific values, and thermal conductances were 117–229% of predicted levels. Body temperatures averaged 36.4°C. The low heat production and high thermal conductance suggest that manatees are poorly adapted energetically to winter water temperatures in much of Florida. These results support behavioural observations of captive and free-living manatees which suggest that 20°C is the minimum suitable water temperature for manatees. Manatees wintering in colder waters are probably in marginal habitat and are most susceptible to cold-related mortality. Warm water refuges reduce energetic maintenance costs and probably temper the effects of occasional periods of severely cold weather, particularly in northern Florida.

INTRODUCTION

Marine mammal adaptations to cold water include a high metabolic rate and a thick blubber layer to conserve heat (see reviews by Ridgway, 1972; Irving, 1973). Some species winter in polar latitudes, and many dive to feed at depths where water temperatures may be 5°C or less. Sirenians, in

contrast, are not well adapted to cold. They are slow-moving aquatic herbivores with a low metabolic rate (Scholander & Irving, 1941), and their distribution is primarily tropical (Bertram & Bertram, 1973).

Energetic information about the West Indian manatee *Trichechus manatus* is of interest because this species ranges into temperate regions. In the southeastern United States, the range is limited by seasonally cold weather (see summary by Husar, 1977), but the winter range has expanded in recent years in association with human development in Florida. Manatees now aggregate at artesian springs or warm water effluents from power plants and factories as far north as Jacksonville (30°21' N) and Tampa Bay (27°51' N; Layne, 1965; Hartman, 1974; Irvine & Campbell, 1978). Manatees arrive at aggregation sites in the autumn as nearby water temperatures fall below the artesian spring or effluent temperatures, and most animals remain until about March when surrounding waters warm to about 20°C (Hartman, 1974, 1979; Powell, 1981; Powell & Waldron, 1981). Relatively few manatees are sighted at wintering sites during warm months (Hartman, 1974; Irvine & Campbell, 1978).

The known shifts in seasonal distribution and the consistent use of available warm water resources suggest that energetic requirements may influence the range limits of manatees. The energetic costs to a manatee of wintering in areas that may be north of historical distribution limits are unknown, but this information is of immediate management concern because manatees are an endangered species. The purpose of this research was to determine the metabolic response of *T. manatus* to different water temperatures and to evaluate the probable energetic loads on manatees at a range of ambient water temperatures in Florida.

The use of product names in this paper does not imply endorsement by the US Fish and Wildlife Service.

METHODS

Three adult manatees, two males and a female, were captured by personnel of the US Fish and Wildlife Service, Denver Wildlife Research Center, and were held at Marineland of Florida. The first manatee (No. 2), captured on 5 March 1976, was held for 18 months and released on 26 August 1977, the same day the second manatee (No. 10) was captured. The third manatee (No. 12) was captured on 19 October 1977.

The manatees were held in a 13.4 m \times 6.7 m \times 2.4 m deep ellipsoid indoor holding tank (1.8×10^5 litres). Small oval tanks measuring 3.8 m \times 2.6 m \times 1.8 m deep (1.9×10^4 litres), were connected at each end of the main tank by a 1.2 m \times 1.1 m door with hinged steel grates. Each small tank was equipped with an independent water supply and drains, although water exchange also occurred through the gate.

The manatees were separated nightly for feeding, and each was fed 28 to 42 kg of head lettuce *Lactuca* sp. and six Sea Tab vitamins (Pacific Research Laboratory Ltd, El Cajon, California). A daily supplement of 0.23 kg of thread herring, *Opisthonema oglinum*, was consistently eaten only by manatee No. 10.

From about April through November, the manatees were held in 20° to 27°C seawater pumped from the ocean. As water temperature (T_w) dropped below 20°C in late autumn, the water supply was switched to a freshwater artesian well; T_w was maintained between 20 and 22°C throughout the winter. Because of the endangered status of the manatees and the difficulty of obtaining test specimens, the experimental animals could be tested only briefly at lower temperatures.

Each manatee was usually weighed (Sampson Scales, Model S-2-12; 907 kg capacity) within 1–9 days before testing. The animals lost weight after capture but stabilised before the metabolic tests (Table 1). Manatees Nos. 10 and 12 gained weight between the winter and summer tests, whereas the weight of manatee No. 2 changed little during testing (Table 1). Manatee No. 12 weighed 383 kg 6 weeks before the 6–10 March 1978 tests, and 396 kg 7 weeks after the tests, so a weight value was extrapolated assuming a linear gain during the period. Metabolic data were collected during August (summer), and January through March (winter). A subject animal was confined to the test tank continuously during a testing period.

For metabolic studies, one small tank was covered with 0.2 mm thick plastic sheet over a rectangular wooden frame atop the tank walls (Fig. 1). Air was withdrawn from the centre of the frame, 7.5 cm above a 1 m diameter board suspended below the frame by bolts. The purpose of the board was to deflect respiration and promote mixing of exhaled and ambient air before entry into the exhaust hose. Minimum clearance between the framework and water was 20 cm. Air volume inside the covered tank was approximately 1.5 m³.

A test sequence usually continued for 2–3 days and commenced after the O₂ consumption rates were stable at ambient T_w (summer \approx 26.5°C; winter \approx 20°C). For summer tests the ocean water system was converted

TABLE 1
Summary of Results of Manatee Metabolic Studies

Manatee	Length (cm)	Sex	Capture wt (kg)	Test wt (kg)	Test dates	Test Tw range (°C)	Core body temp. (°C)	Average metabolic range Tw > 21.5°C mlO ₂ kg h	Average conductance Tw < 21.5°C mlO ₂ kg h°C
No. 12	300	M	465	383	24-27 Jan. 1978	21.2-16.9	\bar{x} = 36.34 SD = 0.31 n = 32		\bar{x} = 2.65 SD = 0.90 n = 36
				389	6-10 Mar. 1978	20.5-14.4			
				433	5-8 Aug. 1978	26.0-22.1	\bar{x} = 36.75 SD = 0.29 n = 39	\bar{x} = 29.71 SD = 8.17 n = 28	
No. 10	319	M	533	466	8-12 Feb. 1978	20.8-18.3	\bar{x} = 36.17 SD = 0.78 n = 46		\bar{x} = 2.93 SD = 0.50 n = 4
				494	2-4 Aug. 1978	26.5-22.7		\bar{x} = 26.92 SD = 7.48 n = 19	
No. 2	278	F	488	359	2-4 Mar. 1977	20.0-15.9			\bar{x} = 1.72 SD = 0.73 n = 18
				359	10-11 Mar. 1977	19.0-17.0			
				356	17-18 Aug. 1977	26.0-24.4		\bar{x} = 20.40 SD = 5.16 n = 4	
Composites:					No. 10 & No. 12 Jan. & Feb. 1978		\bar{x} = 36.41 SD = 0.59 n = 117 \bar{x} = 36.25 SD = 0.63 n = 78	\bar{x} = 27.94 SD = 8.03 n = 51	\bar{x} = 2.38 SD = 0.94 n = 58

n = number of measurements.

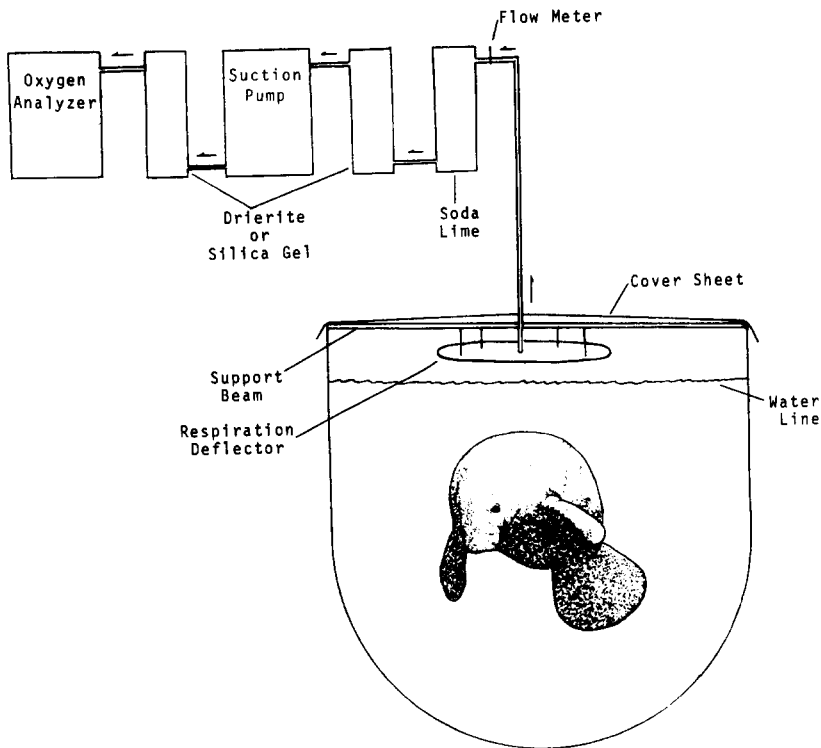


Fig. 1. Diagrammatic view of manatee metabolic test tank and air sample path from tank to O_2 analyser.

to fresh water ($\approx 24^\circ\text{C}$), and then was further cooled (to $\approx 22^\circ\text{C}$) in the experimental tank by the addition of 430 to 560 kg of crushed ice. The gate to the main tank was blocked with a 2.5 cm thick wooden door, but water exchange around the door still occurred and temperatures in the two tanks equalised at a rate of about 1.6°C h^{-1} . For each winter test, $13\text{--}15^\circ\text{C}$ sea water was pumped into the tank, reducing T_w to $\approx 15^\circ\text{C}$ within 1.5 to 2 h. For data analysis, O_2 consumption was only measured after pumping of the cooled water was terminated.

Air and water temperatures were measured with YSI thermistor probes on a 12 channel YSI telethermometer (Model 43). Water temperature was measured 10 cm below the surface and periodically at various depths; movements of the animals caused water mixing. Ambient air temperature (T_a) varied from 7 to 31°C and was similar above and below the tank cover. When T_a was less than 15°C , T_w was held at $20\text{--}21^\circ\text{C}$.

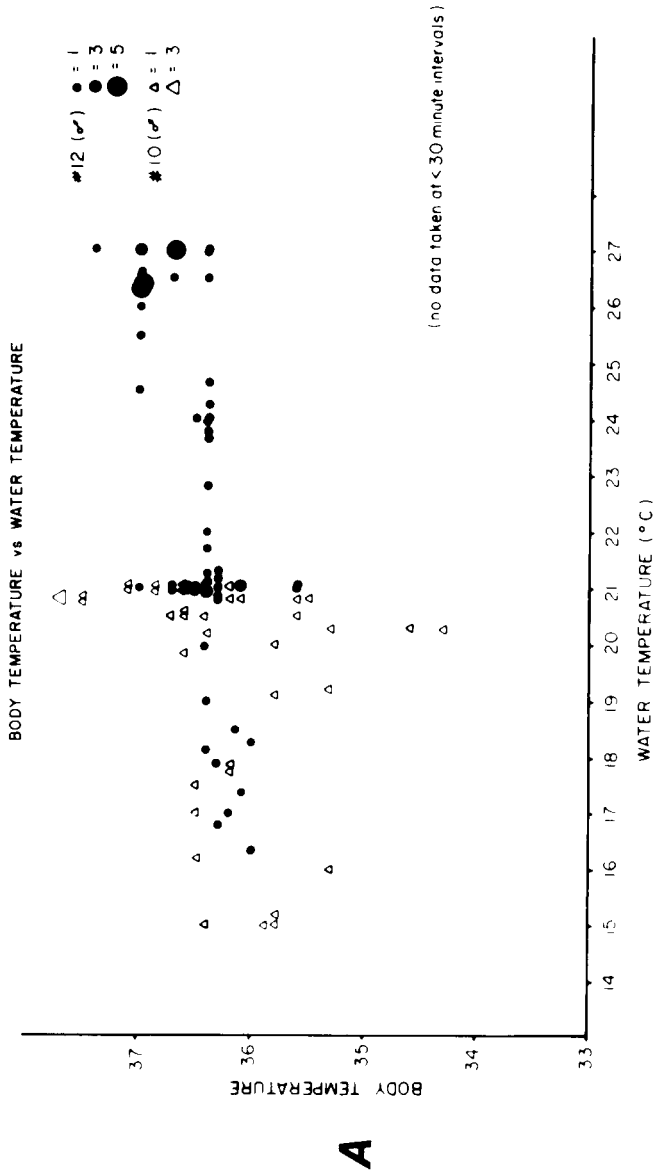


Fig. 2(A). Body temperature of *Trichechus manatus* in different water temperatures. Symbols represent number of measurements.

COMPOSITE METABOLISM vs WATER TEMPERATURE

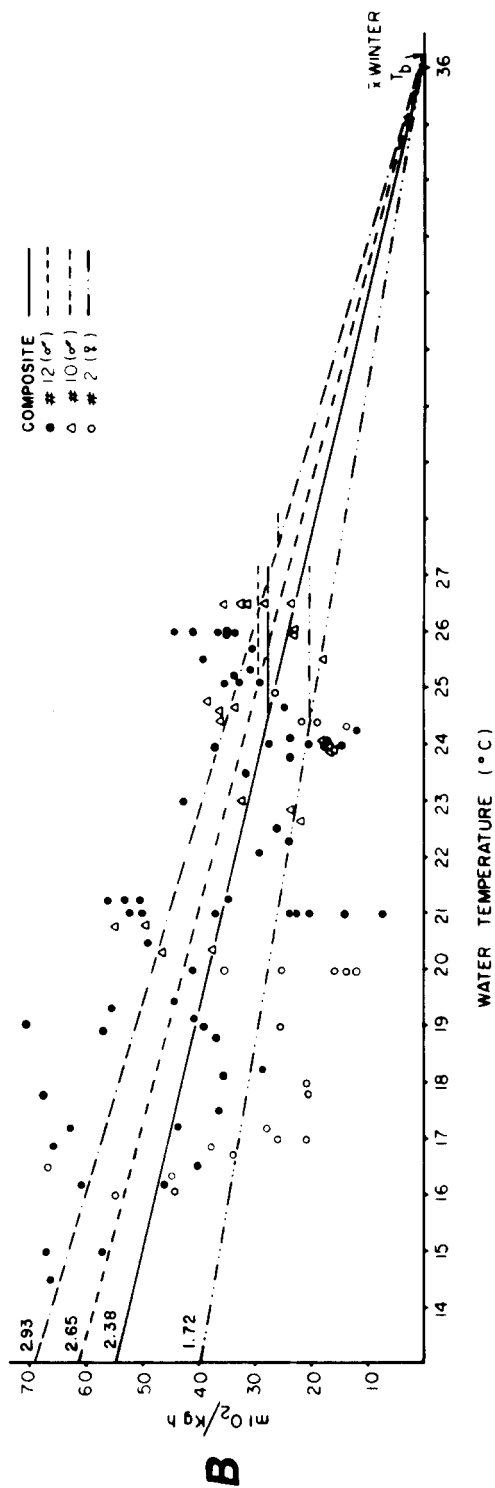


Fig. 2(B). Metabolic rate of *Trichechus manatus* in different water temperatures. Diagonal lines indicate conductance, with average values provided at left. Horizontal lines indicate average metabolic rate (T_w 21.5°C). Thermal neutral zone would be $\approx T_w > 24^\circ\text{C}$.

Oxygen (O_2) consumption was monitored with an open system. Air from the operational tank was drawn with a 1/3 horsepower vacuum pump. Carbon dioxide was removed from the air stream with soda lime, and water vapour was removed with Drierite or silica gel. Flow rates, measured with a Gilmont F1500 flowmeter, were usually from 30 to 40 litres min^{-1} and varied with the quantities of absorbants being used. Oxygen content was measured with a Beckman G-2 paramagnetic oxygen analyser (2% full scale deflection) and recorded on a Honeywell strip chart recorder. The expired air stream was bled into the oxygen analyser at a rate of 200 ml min^{-1} . The oxygen analyser was calibrated with back pressure before each test sequence, and the flow meters were calibrated against known standards. The system was tested for possible loss of expired air by injecting known amounts of nitrogen under the tank cover.

Oxygen consumption rates were used for analysis only when $\Delta\% O_2$ was less than 0.06% for at least 30 min. Each data point (Figs. 2B, 3B) represents average O_2 consumption during a 60 min interval. Tests usually started at 0800–1000 h and terminated at 0130–0300 h the next day, after which the tank was uncovered and the test animal was fed the usual ration of lettuce. Cold water tests were not conducted more often than once every 24 h.

Oxygen consumption values, corrected to STPD, were used to calculate weight specific metabolic rate as $\text{ml } O_2 \text{ kg}^{-1} \text{ h}^{-1}$ ($\Delta\% O_2 \times \text{flow rate (ml h}^{-1}) \times \text{STP, dry, conversion} \times \text{weight}^{-1} \text{ (kg)}$). Thermal conductance, a measure of heat dissipation, and the reciprocal of insulation (Kleiber, 1961; Scholander *et al.*, 1950; McNab, 1970, 1974, 1980), was calculated as $\text{ml } O_2 \text{ kg}^{-1} \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}$. Minimal thermal conductance was calculated as the slope of a line between the average manatee winter body temperature (36.25°C) and the average of O_2 consumption measurements in $T_w < 21.5^\circ\text{C}$ (see discussion in McNab, 1980).

Body temperature was measured with sonic thermistor-transmitters (Smith Root Inc., Vancouver, Wash., Model SR 69T; 60 to 78 kHz) placed in the oesophagus or gastrointestinal tract of the three manatees prior to the tests. For transmitter placement, each manatee was restrained on a wooden platform with foam padding under the animal and five to seven nylon straps across the body. The first transmitter was inserted into manatee No. 2 orally but failed to transmit after apparently being damaged as the animal struggled during the insertion. Subsequent transmitters, a total of two in manatee No. 10 and two in manatee No. 12, were inserted nasally without significant resistance from the animal.

Signals were received on a Smith Root Model TA-25 Sonic Receiver, and transmission pulse rates, which varied with internal body temperature (T_b), were measured with a Smith Root Model PC-74 pulse counter. Pulse rates were translated into temperature from calibration curves ($\pm 0.5^\circ\text{C}$) for each transmitter.

Mean body temperature was calculated from measurements collected at intervals of 30 min or longer, and not within 6 h after the start of feeding. Body temperature measurements were compared by the Mann-Whitney U-test (Siegel, 1956) with $p < 0.05$ the fiducial level of significance. Unless otherwise noted, body temperatures measured by the thermistors are assumed to be core-temperatures.

Rectal temperature was measured with YSI telethermometers (Yellow Springs Instrument Co., Inc., Yellow Springs, Ohio) after the tank was drained, and the animals were rolled on their backs. The animals struggled when a stiff probe (YSI No. 703) was inserted more than 4 cm deep, but allowed up to 15 cm of flexible probe (YSI No. 701) to be inserted. The penetration depth of flexible probes is unknown, however, because they could coil and bend inside the animals.

RESULTS

The average body temperature for all animals was 36.41°C ($\text{SD} = 0.59$; $n = 117$; Table 1). In water below 21.5°C , the T_b of manatee No. 10 ($\bar{x} = 36.17$; $\text{SD} = 0.78$; $n = 46$) was not significantly different from that of manatee No. 12 ($\bar{x} = 36.34$; $\text{SD} = 0.31$; $n = 32$). Both averages were significantly different from the average T_b for manatee No. 12 in warmer water ($\bar{x} = 36.75$; $\text{SD} = 0.29$; $n = 39$). Body temperatures did not change during cold water tests.

Body temperature measurement was strongly influenced by feeding. Lettuce for the manatees was refrigerated at $5.5 \pm 1.5^\circ\text{C}$ until delivered to the manatee tank, and core temperatures of lettuce heads ranged from 12 to 17°C at feeding time. Manatee stomach temperatures dropped as much as 4.7°C within 15 min after feeding started, and remained below preconsumption levels for 5 to 6 h.

Rectal T_b ranged from 27 – 32°C . In one instance, a rectal temperature reading was 32°C , while a stomach transmitter indicated core temperature at 35°C .

Metabolic rate, as determined by oxygen consumption, was measured during 235 h of testing and results are plotted in Figs. 2 and 3. After visual

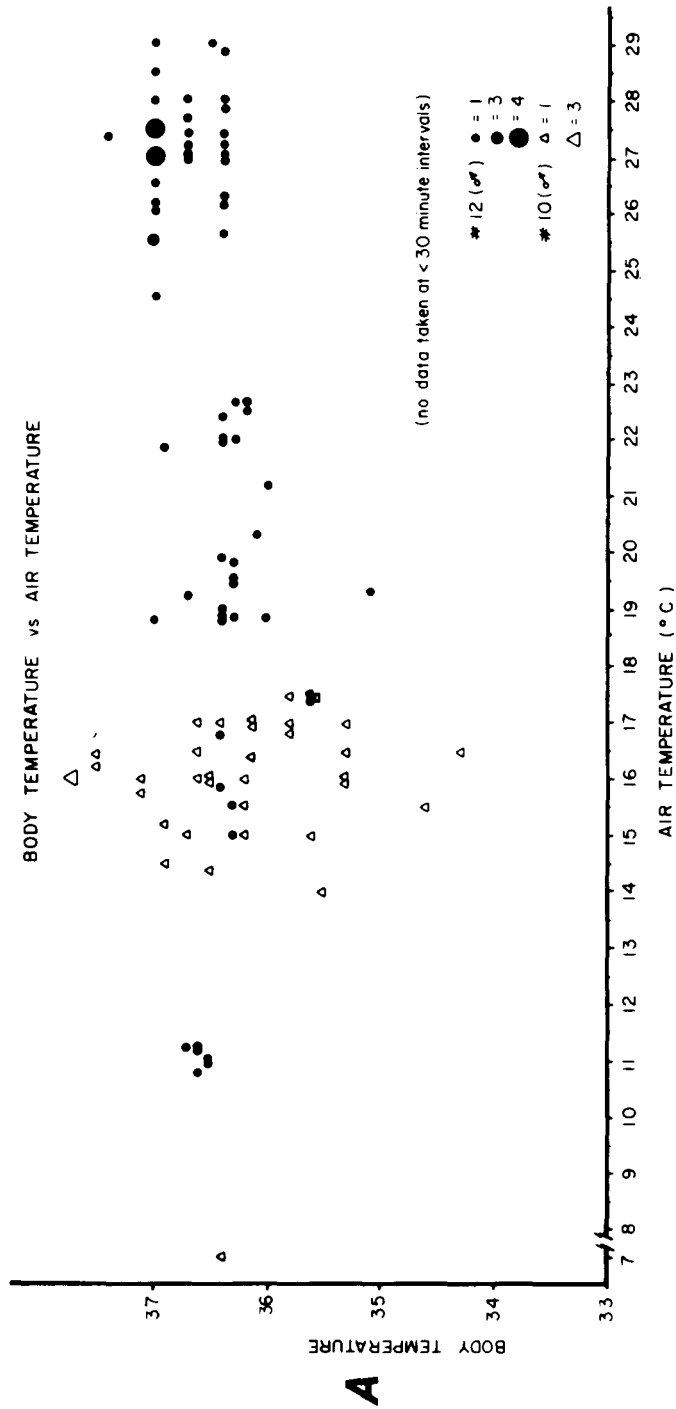


Fig. 3(A). Body temperature of *Trichechus manatus* at different air temperatures. Symbols represent number of measurements.

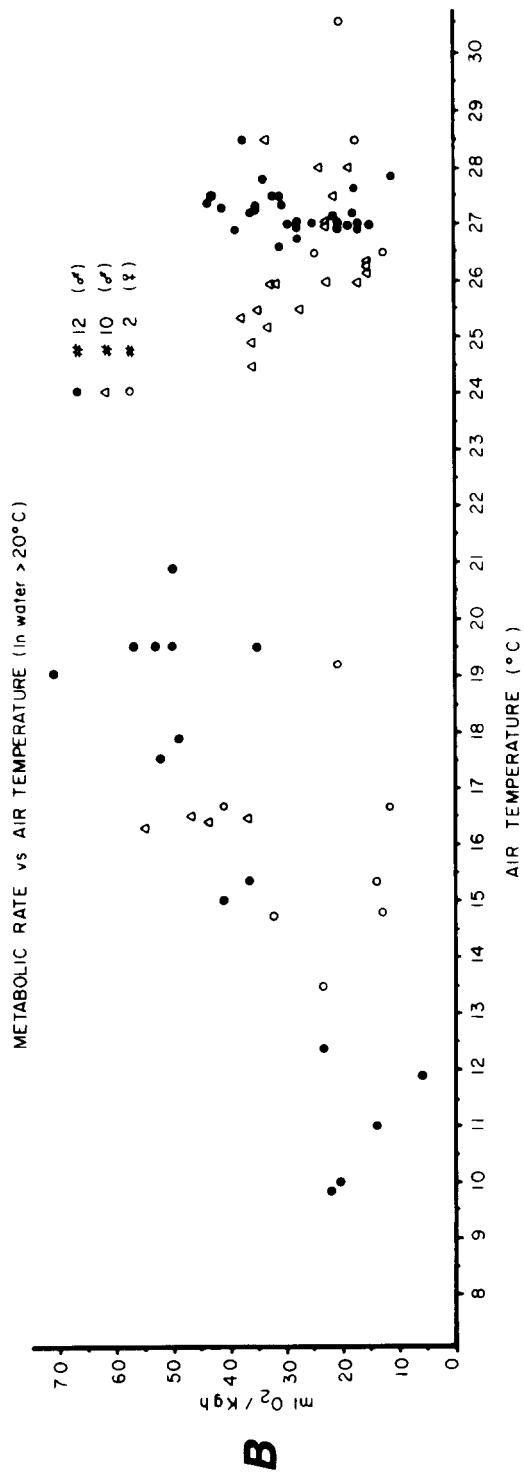


Fig. 3(B). Metabolic rate of *Trichechus manatus* at different air temperatures.

examination of the data in Fig. 2, average metabolic rate was calculated from T_w above 21.5°C and minimal conductance was calculated with temperatures below 21.5°C . The composite average metabolic rate in $T_w > 21.5^\circ\text{C}$ was $27.94 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (SD 8.03 ; $n = 51$) and ranged from 20.40 (SD 5.16 ; $n = 4$) for No. 2 to $29.71 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (SD 8.17 ; $n = 28$) for No. 12 (Table 1, Fig. 2). These values are 14.7% (for No. 2) to 22.3% (for No. 12) of the weight specific metabolism predicted by the equation of Kleiber (1961).

The minimum conductance for all manatees at $T_w < 21.5^\circ\text{C}$ averaged $2.38 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ (SD 0.94 ; $n = 58$) and ranged from $1.72 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ for manatee No. 2 to $2.93 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ for manatee No. 10 (Table 1). These conductance values ranged from 117% (manatee No. 2) to 229% (manatee No. 10) of the weight specific conductance predicted from the formula of Herreid & Kessel (1967). The plot of these values suggests that the average lower limit of thermal neutrality would be about at $T_w = 24^\circ\text{C}$ (Fig. 2B). Neither metabolic rate nor T_b of manatees No. 10 and 12 in $T_w \approx 20^\circ\text{C}$ was obviously affected by ambient air temperature, although relatively few measurements were available at T_a below 15°C (Fig. 3B).

The test procedures did not noticeably affect the behaviour of the manatees, nor the amount of food consumed. No circadian rhythm in metabolic rate was apparent.

DISCUSSION

Manatees have exceptionally low metabolic rates. Most other marine mammals studies have about twice the predicted rates (Irving, 1973), although values for larger species ($> 300 \text{ kg}$) are either not available, or are obtained by extrapolation (e.g. Kanwisher & Sundnes, 1966; Brodie, 1975, 1977). Other mammals with low metabolic rates include Australian marsupials, which average about 70% of predicted eutherian values (Dawson, 1973), neotropical marsupials, which average about 80% of the expected (McNab, 1978), the slow loris which may be as low as 35% of predicted levels (Whittow *et al.*, 1977), and monotremes at $25\text{--}30\%$ of predicted values (Dawson *et al.*, 1979). Metabolic rates for large terrestrial grazers or grazer-browsers approximately fit predicted values and are well above manatee metabolism, but data on large grazers foraging on aquatic plants are not available.

The metabolic rates reported here (17–22 % of expected) were less than one-third of the metabolic rates for West Indian manatees reported by Scholander & Irving (1941). Much of this difference may be because their animals were restrained and exhibited a high respiratory rate during testing. Ambient T_a and T_w were not reported, but also might have influenced the results. Scholander & Irving (1941) predicted that under different conditions the minimal O_2 consumption might be one-third of what they observed.

In the only other tests of sirenian metabolism, the metabolic rates for Amazonian manatees *Trichechus inunguis* were 0.36 times the expected values (Gallivan & Best, 1980). Why the measurements should be well above those from this study is unclear. Data are not available to determine how ecological pressures might influence the metabolic rate of *T. inunguis* in the Amazon drainage.

Because food habits, body size, and climate all affect mammalian energy expenditure (McNab, 1974), the ecological significance of the depressed sirenian metabolism is not clearcut. The low metabolic rate of manatees may be an adaptation of a large tropical animal with a relatively poor quality food source. Limited heat production coupled with high conductance would lessen heat storage, which is a potential problem for marine mammals in tropical water (Irving, 1973). A low metabolic rate should also permit long dives even though manatees lack many of the diving adaptations of other marine mammals (see review by Ridgway, 1972). Similar metabolic adaptations have been predicted for the dugong (Marsh *et al.*, 1978).

The lack of metabolic response to low T_a was only noteworthy because other investigators have reported that manatees respond to a T_a of 10–15°C by moving to warm water sources (Moore, 1951, 1953; Layne, 1965; Hartman, 1979). Compared with body heat lost to the surrounding water, negligible heat would be lost warming inspired cold air. Low T_a may, however, serve as an environmental cue, signalling that T_w will soon fall (Hartman, 1979). Water temperatures in coastal areas of Florida fall and 'adjust' within about 24 to 48 h after the onset of cold weather (Gilmore *et al.*, 1978; Snelson & Bradley, 1978).

The difference in average winter and summer T_b suggests that manatee T_b may vary with season or T_w . Core temperatures of *T. inunguis* in 22–27°C water varied from 32–37°C (J. Kanwisher, pers. comm.), also indicating that manatee body temperature may be quite labile. These T_b measurements are below the value of 37.8°C reported by Morrison &

Ryser (1952) as the average for all mammals, but are similar to values for some other marine mammals (see review by Irving, 1973). The T_b of large hoofed ungulates is often higher (Bligh & Harthoorn, 1965), but can vary with nutritional state (see Whittow, 1971 for review) or exposure to solar radiation (Bligh & Harthoorn, 1965).

The low rectal temperatures obtained from the manatees with inserted probes may indicate the existence of a gradient between core and body surface temperatures. Rectal temperatures of up to 2.2°C less than core temperature have also been reported for large ungulates (see review by Whittow, 1971). In *T. inunguis*, rectal body temperatures of $33 \pm 1^\circ\text{C}$ were recorded in $27\text{--}31^\circ\text{C}$ water (Farmer *et al.*, 1979). Dekeyser (1952, cited in Farmer *et al.*, 1979) noted temperatures of 26.6°C for *T. senegalensis* in $20\text{--}22^\circ\text{C}$ water, but it is uncertain if these represent core body temperatures.

Experimental attempts to measure T_b at different T_w temperatures probably did not provide a comprehensive picture of manatee thermoregulation, because the thermal inertia of a large body mass would probably mask the temporary effects of cold water on core temperature. A large body size also inhibits changes in T_b for other large endotherms (Bligh & Harthoorn, 1965) and large poikilotherms (McNab & Auffenberg, 1976) subjected to temperature changes. The measurements do, however, suggest that free-ranging manatees can probably maintain thermostability at least temporarily during movements from warm water winter refuges into colder adjacent waters. The results presented also indicate that manatee thermostability is not influenced by overnight exposure to cold air. Available data are not sufficient to determine the effects of long-term exposure to cold water or air on T_b .

The decline in T_b associated with feeding occurred because the thermistors recorded gastrointestinal tract temperatures which were influenced by ingestion of cold food or water. It is reasonable to assume that a free-ranging manatee would also incur declines in stomach temperature when eating or drinking, therefore increasing thermal regulatory demands in cold water. The brief gastrointestinal temperature declines attributed to drinking by cetaceans (Hampton & Whittow, 1976) were not noted in this study.

Manatees in the United States thermoregulate behaviourally by moving close to warm water sources during coldest weather, and some animals disperse during intervening periods of mild weather (Moore, 1956; Powell, 1981; Hartman, 1979; Shane, 1981). Individuals may shift

their location to remain in a warm effluent that shifts due to wind conditions (Shane, 1981).

Wintering away from a warm water refuge would be metabolically expensive for a manatee, and energetic costs would increase at higher latitudes where average water temperatures are lower (Fig. 4). Conductance values presented here should be viewed with caution because the large body size of the test animals may not have reached thermal stability in the cold water tests, and conductance predictions are derived primarily from measurements of small animals. Because of the lack of available information, however, the measurements in this study are still useful in providing an indication of the impact of cold water on free-ranging manatees. Manatees that feed 6 to 8 h per day in 23°C water (Hartman, 1979) would probably have to increase their food consumption and feeding time to meet energy demands in 10–15° water. Catabolism of blubber to provide supplementary energy might reduce feeding requirements, but seasonal buildup of fat reserves by manatees has not been reported.

Winter Tw also may influence feeding behaviour. Captive manatees feed erratically in 18–20°C water, and may refuse to eat at 15–18°C (Moore, 1951; Bronwell *et al.*, 1978; Campbell & Irvine, 1981), but some free-ranging manatees leave aggregation sites to feed in areas where water temperatures may average only 15–16°C (Powell & Waldron, 1981; Hartman, 1979; Shane, 1981). Perhaps manatees will forage in cold water ($\leq 16^\circ\text{C}$) if they can later digest in warmer water. Manatees that leave the warm waters of Blue Spring Run to feed (Powell & Waldron, 1981) may be using this strategy. Periodic movements away from other wintering sites have not been reported. Water temperatures in heated effluents and artesian springs used by manatees range from 20 to 23°C (Powell, 1981; Powell & Waldron, 1981; Hartman, 1979; Shane, 1981), which is near the lower limit of thermal neutrality proposed here for manatees.

Campbell & Irvine (1981) have proposed that Tw below 20°C are unsuitable for manatees. Historical winter range limits (Moore, 1951; Hartman, 1979) approximately correspond with the minimum 20°C isotherm (Fuglister, 1947), and with areas where cold-related mortalities occur (Bangs, 1895; Cahn, 1940; Hamilton, 1941; Krumholz, 1943; Layne, 1965). Manatee tolerance to cold is uncertain, but cold-related die-offs have always followed periods of severely cold weather (e.g. 0°C air temperatures reaching to southern Florida). Warm water refuges probably reduce the energetic costs of thermoregulation during cold

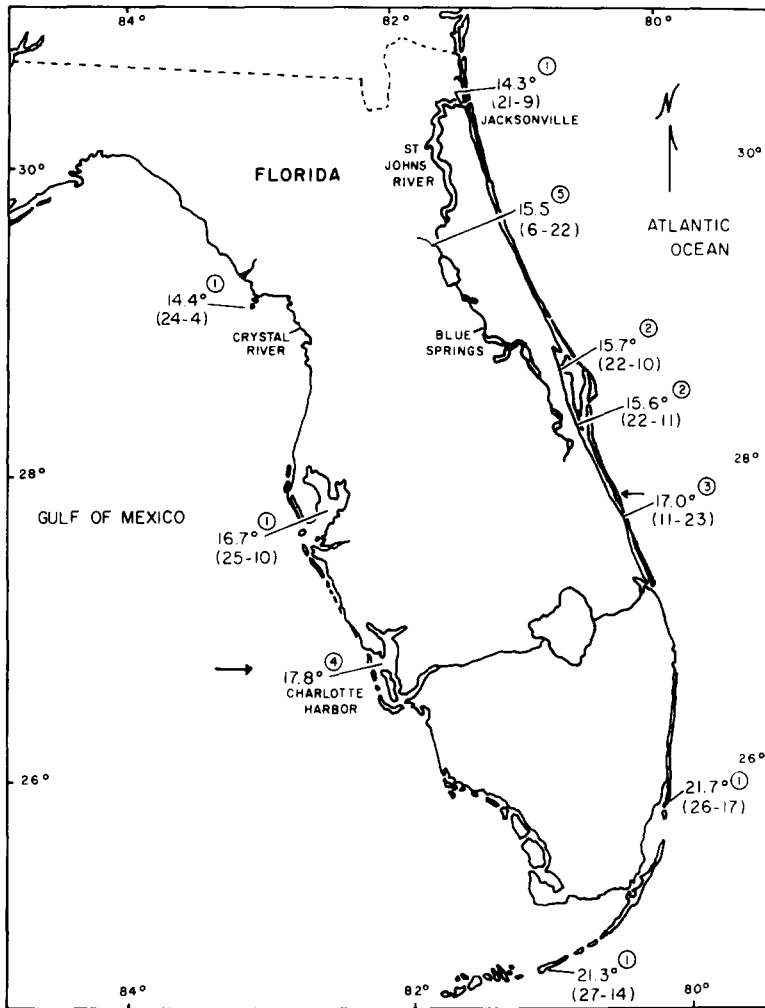


Fig. 4. Average January temperatures ($^{\circ}\text{C}$) at different locations in Florida, with range in parentheses. Circled numerals indicate data sources. (1) U.S. Department of Commerce (1972). (2) Brevard County, Florida Department of Health and Environmental Regulations, Merritt Island, Florida, unpublished data. (3) Vero Beach Municipal Power Plant, Vero Beach, Florida (intake temperatures), unpublished data. (4) Wang & Raney (1971). (5) Water Resources Data for Florida 1967-1977. U.S. Geological Survey Water-data Reports. Tallahassee, Florida, USA. Historical winter range (Moore, 1951) is indicated by \rightarrow ; current winter range extends north to Jacksonville on the Atlantic Coast and Crystal River on the West Coast (Hartman, 1974).

weather, but in northern areas, artificial warm water sources may produce insufficient heat during severely cold weather (Campbell & Irvine, 1981).

Although the present study provides new information about what may be the standard metabolic rate and approximate lower limit of thermal neutrality of manatees, more information is needed to show clearly the effects of low temperatures. The conductance calculations reported here were probably only relative measures because the animals were underweight and low T_w ($\leq 20^\circ\text{C}$) were not stabilised during testing. Metabolic tests of capture-weight manatees at constant low- T_w would more precisely indicate minimum thermal conductance.

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